COMPARATIVE ANATOMY AND SYSTEMATICS OF PICRODENDRON, GENUS INCERTAE SEDIS *

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A GENUS OF SMALL dicotyledonous trees which occurs on some of the Bahama Islands and Greater Antilles, *Picrodendron* Planchon has been poorly understood for most of its long history. Before it was recognized as a distinct genus, *Picrodendron* had been confused with three different genera: *Juglans* L., *Rhus* L., and *Schmidelia* L. (= *Allophylus* L.). Moreover, it has been considered as a member of or having affinities with Anacardiaceae (Macfadyen, 1837), Sapindaceae (Richard, 1845), Simaroubaceae (Planchon, 1846; Bentham & Hooker, 1862; Urban, 1920; Moscoso, 1943), Juglandaceae (Grisebach, 1859), Burseraceae (Grisebach, 1866), Terebinthaceae (Hallier, 1908), Picrodendraceae (Small, 1917; and numerous recent authors), Euphorbiaceae (Fawcett & Rendle, 1917; Thorne, 1968; Webster, 1975), and Bombacaceae (Hallier, 1923). Picrodendraceae has been variously placed in Juglandales (Cronquist, 1968; Hutchinson, 1973), Rutales (Scholz, 1964; Takhtajan, 1966), and Euphorbiales (Novák, 1961; Takhtajan, 1969).

This study of the vegetative anatomy of *Picrodendron* and some of its putative relatives has been undertaken in order better to understand its natural relationships. Despite the number of anatomical studies in the literature (Jadin, 1901; Solereder, 1908; Boas, 1913; Webber, 1936; Heimsch, 1942; Record & Hess, 1943; Metcalfe & Chalk, 1950), our information on the anatomy of *Picrodendron* is still incomplete; for example, nodal and petiolar anatomy has apparently never been described. Furthermore, with the exception of Record and Hess (1943), who discussed *Picrodendron* in a family by itself, other anatomists have compared *Picrodendron* only with members of Simaroubaceae, although sometimes doubting that its anatomical similarities with the subfamily Irvingioideae reflected a natural relationship (Boas, 1913; Webber, 1936; Heimsch, 1942). In this paper, the anatomy of *Picrodendron* is described in detail; it is compared to that of its putative relatives and, for the first time, to that of Euphorbiaceae.

DESCRIPTION AND DISTRIBUTION

Picrodendron Planchon. Deciduous trees or shrubs with shaggy bark. Leaves alternate, long-petiolate, trifoliolate; petiole minutely pubescent; stipules present, very small, setiform, caducous or persistent; leaflets leathery, oblong-elliptic, entire, pinnately veined, subglabrous above, pubescent beneath, petiolulate; petiolules jointed at the base. Flowers unisexual, plants dioecious. Male flowers sessile or on a small pedicel, solitary

or clustered on simple or sparingly branched spikes arising from the axils of fallen leaves of the previous season's shoots, subtended by (1–)3(–7) unequal, imbricate bracts; perianth lacking; stamens 3–numerous on a hemispherical receptacle, forming a globose head; filaments free, short; anthers ellipsoidal, minutely pubescent above, 2-locular, basifixed, dehiscing by longitudinal slits, extrorse; pollen spinose-verrucate; no vestige of an ovary. Female flowers solitary, on slender pedicels arising from the axils of leaves of the current season; the pedicels finely pubescent; sepals 4(–5), lanceolate, unequal, free, valvate, with small glands at the base, sometimes obscurely toothed or ciliate; petals, staminodes, and disc all lacking; ovary superior, 2-locular, sessile, gradually narrowed into a stout, deeply 2-lobed style; stigmas with revolute margins; ovules 2 in each loculus, pendulous from a hemispherical placenta at the top of the loculi, anatropous; raphe ventral; integuments 2; obturator reddish-brown, one per ovule, arising from the placenta and closely covering the micropyle, withering upon maturation of the seed. Fruit a globose drupe; exocarp thin, fleshy, orange, or yellow to greenish-yellow, containing numerous vesicles filled with bitter juice; endocarp hard, indehiscent, obscurely 4-angled. Seed 1 per fruit by abortion, occupying most of the fruit, globular; cotyledons much corrugated, reflexed; radicle superior; endosperm lacking. (The preceding description has been collated from the following authors: Adams, 1972; Britton & Millspaugh, 1920; Engler, 1931; Fawcett & Rendle, 1917, 1920; Grisebach, 1859; Hutchinson, 1973; Planchon, 1846; Small, 1911, 1917; and Willis, 1973). A chromosome count of $2n = 48$ has been reported by Fritsch (1972).

Descriptions of *Picrodendron* in the above-mentioned works contain some contradictions and/or differences in interpretation. Given the small and often ephemeral nature of the stipules, it is not surprising that some authors (e.g., Grisebach, 1859) described the plants as estipulate. The male inflorescence has been described as "a catkin" or "amentaceous" by authors supporting a relationship to the Juglandales (Grisebach, 1859; Small, 1917; Hutchinson, 1973). Alternatively, male inflorescences have been described as "stalked axillary spikes" (Fawcett & Rendle, 1917) or "strict catkin-like pseudo-racemes or narrow thyrses" (Willis, 1973). Small (1917) suggested that the hemispherical receptacle of the male flowers might be formed by the coherence of the lower parts of the filaments, although most authors describe the filaments as free. Fawcett and Rendle (1917) erroneously reported an inferior ovary for *Picrodendron*, but later corrected this mistake (1920). Pax and Hoffmann (1931) and Engler (1931), citing Fawcett and Rendle's earlier paper, unwittingly continued this error. The ovary is unquestionably superior. Only Fawcett and Rendle (1917, 1920) and Engler (1931) mentioned the ventral raphe, the obturator, and the presence of glands on the sepals of female flowers.

Until recently *Picrodendron* had been divided into three species as summarized by Small (1917):

1) *P. baccatum* (L.) Krug & Urban, from Jamaica, the Cayman Islands, and Swan Islands.

2) *P. macrocarpum* (A. Rich.) Britton, from Cuba and the Bahamas.

3) *P. medium* Small, from Hispaniola.

These species were separated largely on characters of the leaves and fruit. William T. Gillis (1974, and pers. comm.), however, has concluded from field and laboratory studies that, even though these plants vary, they do not do so in any way which would uphold the division of the genus into three species. He has therefore decided (1974) that the genus is monotypic and that the correct name for the single species is *P. baccatum* (L.) Krug & Urban.

The distribution of *Picrodendron* is striking in that it is present in Cuba, Jamaica, and Hispaniola, but is absent from Puerto Rico, a distribution shared by 20 other genera in the Greater Antilles (Howard, 1973). *Picrodendron* inhabits arid, rocky (usually limestone) areas, maritime rocks, margins of saline water in deltas, or the landward margins of mangrove formations.

MATERIALS AND METHODS

Specimens used in this investigation and their documentation are listed in TABLE 1. For the most part, standard techniques were used in tissue preparation and sectioning, and are described in detail elsewhere (Hayden, 1976).

Diagnostic characters used to describe leaves were selected from Esau (1965) and Fahn (1974), among other sources. Terminology used in characterizing leaf architecture follows that proposed by Hickey (1973). Characters and terminology employed in describing wood were selected from Tamolang *et al.* (1963) and Tippo (1941), and are essentially in accord with those recommended by the Committee on Nomenclature, International Association of Wood Anatomists, *International Glossary of Terms Used in Wood Anatomy* (1957).

ANATOMICAL DESCRIPTION

Picrodendron baccatum

INTERNODE. Epidermis of the young axis was not observed; in the specimen examined (*Gillis 10975*) it had already been replaced by a periderm of superficial origin. Scattered among the parenchyma cells of the cortex are idioblasts containing either an amber-colored substance,[1] mucilage, druses, or prismatic crystals. Some of the phloem parenchyma cells contain druses, prismatic crystals, or an amber-colored substance. Groups of thick-walled fibers occur external to the conducting cells of the phloem, forming an incomplete ring around this tissue. Xylem, at least after some secondary growth has occurred, is in the form of a complete ring. Imperforate tracheary elements are thick walled, and pores are either solitary or in short radial multiples. Tangential diameters of pores range

[1] This substance turns dark gray or black in 4 percent iron alum.

TABLE 1. Specimens examined.[a]

SPECIES	COLLECTOR	LOCALITY [b]	TYPE OF SPECIMEN [c]	XYLARIUM [d]	HERBARIUM VOUCHER [e]
Picrodendron baccatum (L.) Krug & Urban	Gillis 10893	Florida	w* l* t*	—	FTG
Picrodendron macrocarpum (A. Rich.) Britton	Gillis 10975	Florida	w* l* t*	—	FTG
	Gillis 6963	Florida	w* l* t*	—	FTG
Picrodendron medium Small	Stadtmiller 171	Haiti	w	SJRW 19616	—
Juglans major (Torrey) Heller var. glabrata Manning	Frejnik s.n.	Mexico	w (slide only)	USW[f] 19742	—
Desbordesia sp.	commercial sample	Gaboon	w	SJRW 12804	—
Irvingia gabonensis (Aubrey-Lecomte) Baillon	commercial sample	Gaboon	w	SJRW 12841	—
Irvingia malayana Oliver ex Benn.	—	—	w (slide only)	USW[g]	—
Klainedoxa buesgenii Engler	C. Donis 405	Congo	w	USW 24403	BR
Klainedoxa gabonensis Pierre ex Engler	—	Belgian Congo	w	USW 18322	BR
	—	—	w (slide only)	USW[h]	—
Oldfieldia africana Bentham & Hooker f.	commercial sample	Sierra Leone	w	USW 19900	—
Celaenodendron mexicanum Standley	Ortega 35	Mexico	w	USW 3886	—
Piranhea longepedunculata Jablonski	Breteler 5096	Venezuela	w	USW 35682	MER, NY, U, US, WAG
Piranhea trifoliata Baillon	Capucho 493	Brazil	w	USW 22377	IAN
	A. Ducke s.n.	Brazil	w	USW 31485	MAD
	—	—	w (slide only)	USW[i]	—

[a] Additional information concerning the *Picrodendron* specimens is contained in APPENDIX 1.
[b] Political units are stated as originally shown.
[c] w = wood, l = leaf, t = twig; an asterisk (*) indicates a fluid-preserved specimen.
[d] Xylarium abbreviations follow Stern (1967).
[e] Herbarium abbreviations follow Holmgren and Keuken (1974).
[f] Originally received at USW from Archie F. Wilson Collection (907) as *Juglans pyriformis*.
[g] Received at USW from KEPW.
[h] Received at USW from PFPW.
[i] Received at USW from MERW.

from 17 to 38 μm. Vascular rays appear to be either uni- or biseriate. Pith cells are roughly circular in cross section and have sclerified walls. Prominent intercellular spaces are present in the pith. Some pith cells have evident cytoplasm while others are filled with an amber-colored substance which renders other cytoplasmic contents difficult to detect. Neither crystals nor secretory cavities were observed in the pith.

Bark of twigs in their second season of growth consists of periderm, cortex, primary phloem, and secondary phloem; cells with amber-colored deposits are frequent throughout these four tissues. Groups of thick-walled fibers are scattered here and there in the secondary phloem. Each group of fibers is surrounded by strands of sclerified crystalliferous cells which are in turn surrounded by cells containing amber-colored deposits. The extraxylary fibers formed during primary growth are thus easily distinguished from those formed during secondary growth since only the latter are surrounded by crystalliferous cells. Neither secretory canals nor cavities were observed in the bark at any stage of development.

NODE AND PETIOLE. The node is characterized by three leaf traces, each of which departs from a separate gap in the stele as it enters the petiole. Serial sections from an internode to the super-adjacent node reveal that the median trace is first to separate from the stele, at about 3.5 mm. below the insertion of the petiole. Two lateral traces become separate from the stele at approximately 2.5 mm. below the node. At this level the traces are embedded in cells of the cortex. External to each trace there are a few groups of thick-walled fibers.

At the level in which the leaf traces pass into the petiole, several changes become apparent. First, leaf traces are embedded in a ground-mass of small, tightly packed parenchyma cells which mark the position of the future leaf abscission zone; these cells are distinguished from cells of the normal stem cortex by their smaller size and the absence of idioblasts. Second, the three gaps in the stele are nearly closed. Finally, groups of fibers external to the leaf traces are no longer present but are situated between the leaf traces and the stele.

At the proximal end of the petiole, the three leaf traces are arranged in the form of a broad V. Although no extraxylary fibers are associated with the traces at first, they reappear at higher levels. Progressing up the petiole, one observes the following changes within approximately the first 5 mm.: first, the lateral traces break up, each forming two or three traces of unequal size; then, some of the smaller traces become inverted and displaced to a position between the tips of the V; finally, all of the traces expand somewhat and form a more or less continuous but irregularly shaped ring of vascular tissue. The configuration attained at this level remains essentially unchanged throughout the petiole except at the extreme distal end (see below).

There are two layers of epidermal cells surrounding the petiole. The ground tissue external to the vascular tissue is similar to the cortex of the stem, and includes the same types of idioblasts. Groups of thick-

walled fibers form a discontinuous ring surrounding the vascular tissues. Phloem is external; xylem is internal. At the center of the petiole there are some sclerified parenchyma cells similar to the pith cells of the stem.

At the distal end of the petiole, the vascular tissues branch and enter the three leaflets. Mucilage cells become so numerous that they form the predominant cell type in the ground tissue surrounding the vascular tissues. In some instances portions of cell walls between adjacent mucilage cells are lacking, thus forming short (3–4 cells long) mucilage cavities. The groups of extraxylary fibers begin to disappear prior to the branching of the vascular tissue into individual vascular bundles. These fibers reappear in the petiolules. Five vascular bundles, three from the lower part and two from the upper part of the ring of petiolar vascular tissue, enter the petiolule of the middle leaflet. This results in two groups of vascular bundles located at opposite sides of the petiole; each of these groups of bundles enters the petiolule of a lateral leaflet. Within each petiolule the vascular bundles are arranged in the form of a broad U; this same vascular pattern is carried into the primary vein of the leaflet blade.

Leaf blade. Leaves of *Picrodendron* are trifoliolate. Leaflets have a smooth upper surface and entire margins. Thick-walled, unicellular trichomes are present on the abaxial surface, most frequently below the primary and secondary veins but with a few below higher order veins. Venation is pinnate; specifically, either brochidodromous or reticulodromous (Figures 1, 2). Areoles are well developed, random to partially oriented, and quadrangular to polygonal. Veinlets are simple, either linear or curved, or infrequently branched once. Marginal ultimate venation is fimbriate. Neither glands nor extrafloral nectaries are present.

The cuticle is thin, approximately 4 μm. thick over the primary vein and at the margin, and 2 μm. thick over the remainder of the laminar surface. Abaxially, the cuticle is thinner and sometimes difficult to detect. Both epidermides are uniseriate (Figure 3). Cells contain an amber-colored substance and, rarely, prismatic crystals. In surface view epidermal cells of both leaf surfaces are roughly squarish to rectangular (up to two or three times longer than broad) and mostly 15–35 μm. long. All walls are straight and smooth. In cross section, cells of the upper epidermis are roughly squarish to rectangular and 20–25 μm. tall; cells of the lower epidermis are similar, but only 10–15 μm. tall. Stomata are restricted to the abaxial surface. Subsidiary cells have their long axes parallel to the long axis of the pore, i.e., the stomatal apparatus is paracytic. Apparently a cell division may take place in subsidiary cells and, depending on the plane of division, the division results in paired subsidiary cells in two possible orientations on each side of the guard cells (Figure 4): if the plane of division is parallel to the long axis of the pore, the result is a pair of subsidiary cells with their long axes also parallel to the pore; if the plane of division is perpendicular to the long axis of the pore, the result is a pair of somewhat triangular cells adjacent to each guard cell. Guard cell pairs range from 27 to 34 μm. long and from 12 to 24 μm. wide,
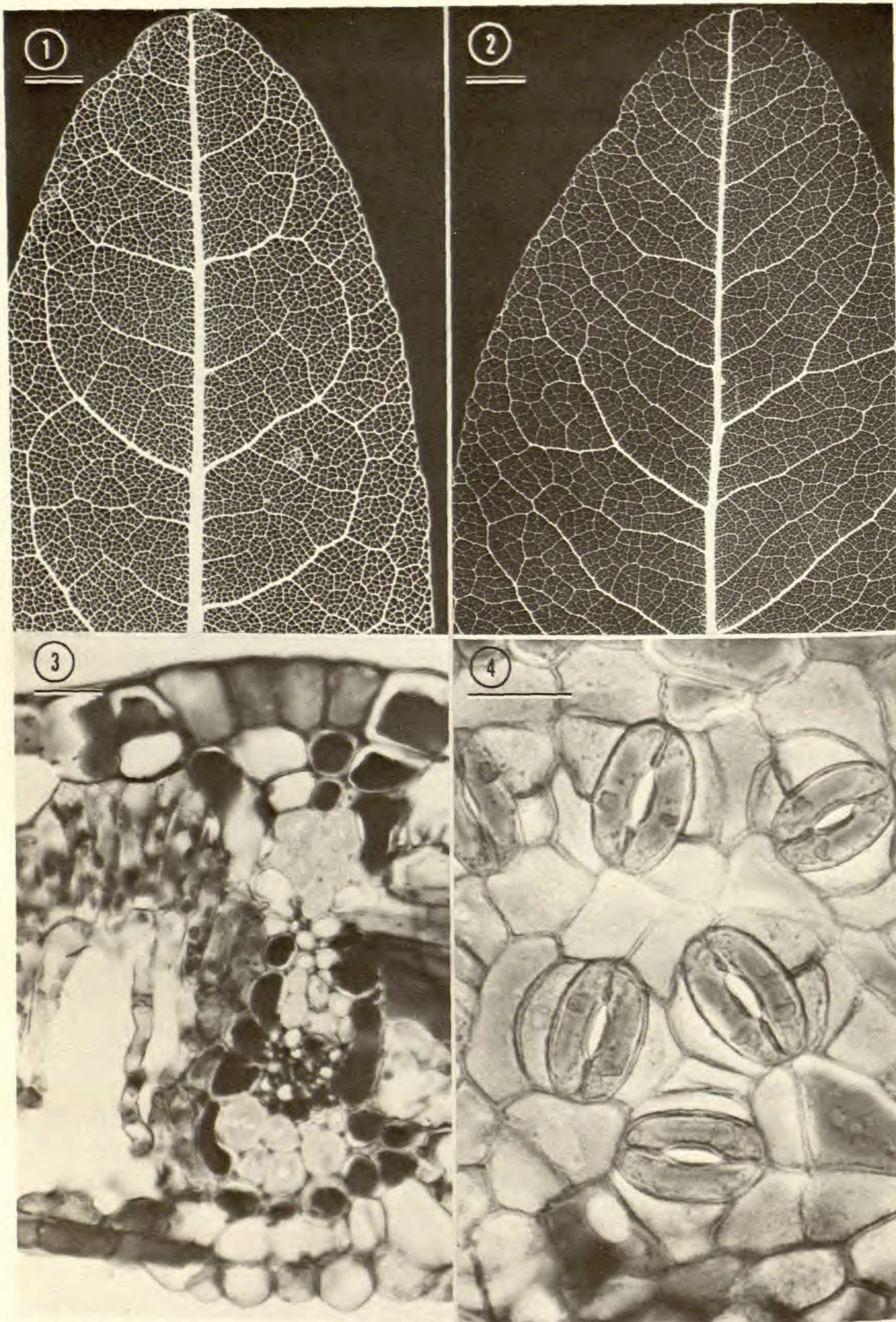
FIGURES 1–4. **Picrodendron baccatum:** 1, leaflet clearing showing brochidodromous venation, *Gillis 10975*; 2, leaflet clearing showing reticulodromous venation, *Gillis 6963*; 3, cross section of leaflet showing a small vein with a bundle sheath and bundle sheath extension, *Gillis 10893*; 4, paradermal section of leaflet showing stomata and various configurations of subsidiary cells, *Gillis 10893*. Figs. 1, 2, bar = 2.5 mm.; Figs. 3, 4, bar = 20 μm.

and have an average length to width ratio of 1.58. Guard cell walls are unevenly thickened: the upper portion of the anticlinal wall adjacent to the pore and the inner periclinal wall are thickest; the lower portion of the anticlinal wall adjacent to the pore is somewhat thinner; and the remaining walls are only as thick as those of other epidermal cells. Typically a larger outer ledge and a smaller inner ledge of cuticle are present. Each guard cell is reniform, and guard cell pairs are elliptical in face view.

Leaflets are dorsiventral and possess a heterogeneous mesophyll (FIGURE 3). Palisade mesophyll cells are of different lengths and are arranged in 1–4 rows of cells. Most spongy mesophyll cells are elongated vertically and are situated near the veins, with very few cells present in the center of the areole. Consequently, very large intercellular spaces are formed between the veins. Some shorter and more "normal" looking spongy parenchyma cells are present in a thin layer near the lower epidermis.

In cross section, the primary vein possesses a semicircular arc of vascular tissue. Patches of conducting cells of the xylem separated by small groups of parenchyma cells are situated on the inner (adaxial) portion of the arc. Phloem is situated below the xylem on the outer (abaxial) portion of the arc. There are groups of thick-walled fibers external to the phloem and also between the two ends of the arc of vascular tissues, thus enclosing a pithlike region of parenchyma cells. These parenchyma cells have sclerified walls and may contain an amber-colored substance. Among the parenchyma cells of the ground tissue surrounding the vascular tissues of the midvein, there are idioblasts which may contain an amber-colored substance, mucilage, druses, or prismatic crystals. Druses, prismatic crystals, and cells containing an amber-colored substance are also found in the phloem.

Secondary and higher order veins are all vertically transcurrent (FIGURE 3). The xylem (adaxial) and phloem (abaxial) are situated between two groups of thick-walled fibers. Parenchymatous bundle sheath cells surround the conducting cells and the fibers. Cytoplasm and nuclei are evident in some bundle sheath cells; others contain an amber-colored substance or crystals. Veins are connected to both epidermides by a one- or two-cell-thick bundle sheath extension. The parenchymatous bundle sheath extension flares out near each epidermis to such an extent that it may be wider than the vein itself. Cells of the bundle sheath extension frequently contain druses or prismatic crystals.

Ultimate veinlets do not possess fibers, phloem cells, or a bundle sheath extension to the lower epidermis. Such veinlets consist of a single row of xylem elements surrounded by a parenchymatous sheath, and are connected to the upper epidermis by a single row of parenchymatous bundle sheath extension cells. Within approximately 30 μm. of the termination of the veinlet, the upper bundle sheath extension is lost. The veinlet ends abruptly as a single xylem element surrounded by two parenchymatous bundle sheath cells.

WOOD. Distinct growth rings are not present in the wood of *Picrodendron*. Pores are distributed as follows: 62 percent solitary, 34 percent in radial multiples of 2–13 cells, and 4 percent in clusters of 3–10 cells (FIGURE 5). Pore outlines are circular or slightly elliptical. Vessel element walls have an average thickness of 5.2 μm. and a range of 3.0–7.5 μm. The moderately small pores have an average tangential diameter of 88 μm., with a range of 45–153 μm. Perforation plates are exclusively simple and have a narrow border. Intervascular pitting is alternate; the pits are circular to polygonal and show circular to elliptical inner apertures included within the pit border. Sometimes inner apertures of two adjacent pits coalesce, forming a groove on the inner surface of the vessel wall. Intervascular pits are medium-sized; average vertical diameter is 8.1 μm., with a range of 4.0–10 μm. The moderately short vessel elements (FIGURE 8) range from 124 to 494 μm. long, with an average length of 299 μm. Vessel elements are usually ligulate. Vessel element end wall angles range from 16 to 90°, with an average inclination of 57° from the vertical. Thin-walled tyloses were observed in sections of the heartwood; otherwise vessel elements are without deposits.

Imperforate tracheary elements have very thick walls and simple or faintly bordered pits with crossed inner apertures which are approximately 2.5–3.0 μm. long. These moderately short imperforate elements have an average length of 872 μm., with a range of 538–1700 μm. The very narrow lumen of imperforate tracheary elements frequently contains amber-colored deposits.

Rays are both uniseriate and multiseriate. Both types of rays are heterocellular, consisting of procumbent cells near the center of the ray and 1–3 rows of square to short erect cells at the margin of the ray (FIGURES 6, 7). Marginal ray cells are frequently disjunctive. Uniseriate rays average 16 μm. wide and 168 μm. (2–9 cells) high. Multiseriate rays are mostly biseriate, but there are some triseriate rays. Multiseriate rays average 30 μm. wide and 293 μm. tall. Multiseriate rays have uniseriate wings of 1–4 cells, and in some cases two superposed multiseriate rays may be connected by their uniseriate wings. Pit-pairs between ray cells and vessel elements vary from half-bordered to simple and have an average vertical diameter of 6.5 μm. The width of the pit-pairs varies from 5.4 to 11 μm., so the overall shape ranges from circular to elliptical. Ray cells frequently contain an amber-colored substance. No crystals were observed in ray cells.

The amount and distribution of axial xylem parenchyma varies somewhat in the different specimens examined, and even in different parts of the same specimen. Paratracheal parenchyma is mostly scanty, but sometimes vasicentric, or approaching aliform. Apotracheal parenchyma is diffuse, diffuse-in-aggregates, or in poorly or well-defined bands up to 10 cells wide. Axial xylem parenchyma cells are of two distinct sizes: tall cells (average height 67 μm.) and short cells (average height 23 μm.). Tall axial xylem parenchyma cells have contents similar to ray cells, whereas the short cells contain an anisotropic prismatic crystal and have
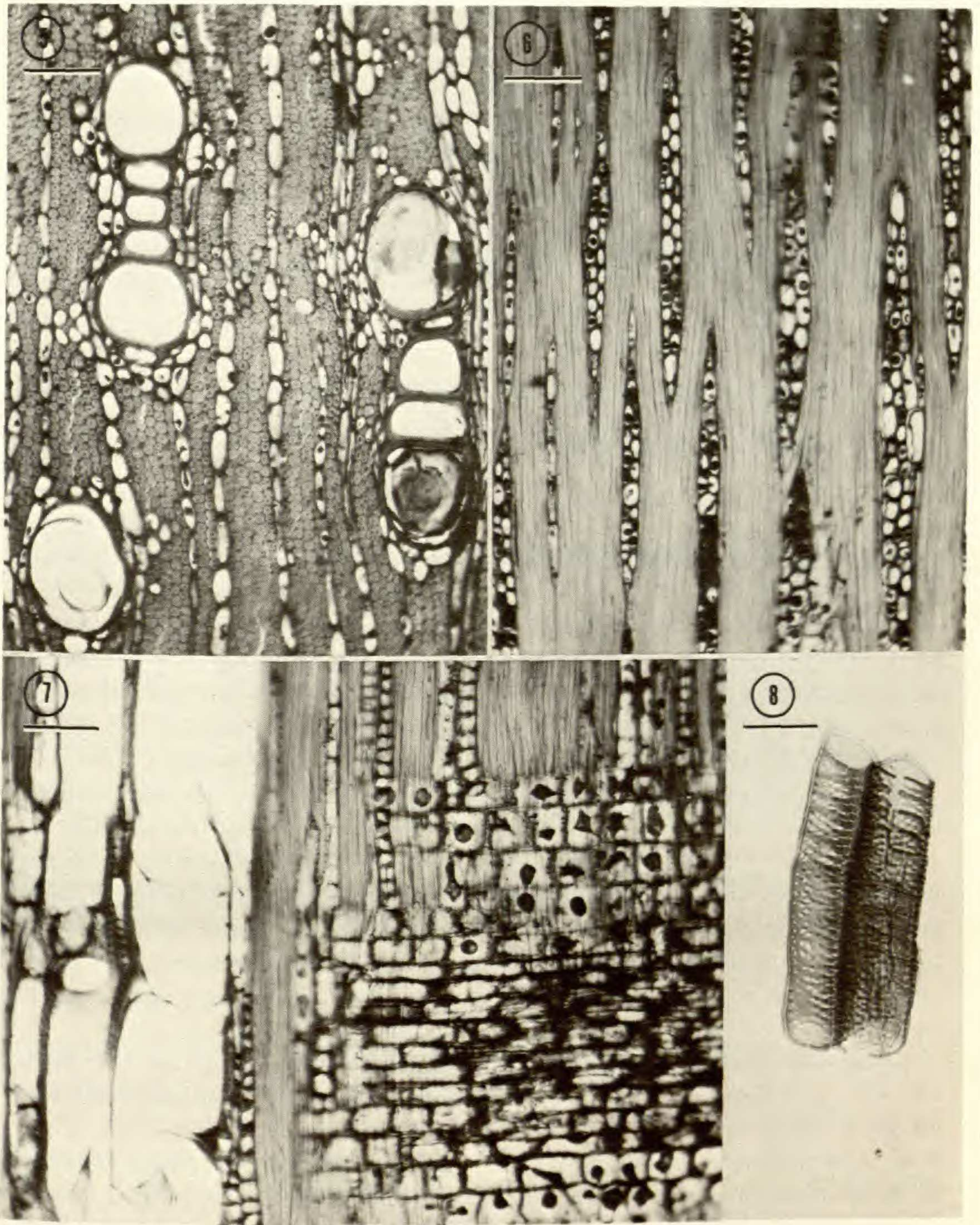
FIGURES 5–8. **Picrodendron baccatum:** 5, cross section of wood showing a solitary pore and two radial multiples, *Stadtmiller 171* (SJRW 19616); 6, tangential section of wood showing uni-, bi-, and triseriate heterocellular rays, *Stadtmiller 171* (SJRW 19616); 7, radial section of wood showing a heterocellular ray, *Stadtmiller 171* (SJRW 19616); 8, vessel elements from macerated wood, *Gillis 6963*. Figs. 5–8, bar = 80 μm.

sclerified walls. Strands of axial xylem parenchyma cells average 418 μm. long and may consist of 6–8 tall cells, 16–18 short cells, or an intermediate number of cells since both types of cells may occur in the same strand. Pits between vessel elements and xylem parenchyma cells are half-bordered.

DISCUSSION

Aside from a comparison of the anatomy given above with that contained in earlier literature, data on the anatomy of *Picrodendron* can be applied to two different taxonomic questions: Is there any anatomical evidence for more than one species in the genus? Moreover, what evidence does the anatomy of *Picrodendron* provide towards the elucidation of its relationships?

COMPARISONS WITH EARLIER ANATOMICAL RESULTS

In several respects the results reported here differ from descriptions contained in earlier literature. Mucilage lacunae were not observed in the pith as reported by Jadin (1901), nor were mucilage cells observed in the mesophyll as reported by Boas (1913). Contrary to Metcalfe and Chalk (1950), I do not interpret the mesophyll as homogeneous since there are large intercellular spaces in the lower half of the mesophyll (FIGURE 3) which are not found among the palisade cells, and further, not all of the cells of the lower half of the mesophyll are vertically elongated. For these reasons I feel justified in calling the mesophyll heterogeneous.

Webber (1936) interpreted the imperforate tracheary elements in the wood of *Picrodendron* as libriform wood fibers, implying the presence of simple pits. My investigations show that pits on these elements are either simple or have a faint border. Therefore, I have joined Heimsch (1942) and Record and Hess (1943) in calling these cells merely imperforate tracheary elements, avoiding the difficult decision in distinguishing fiber-tracheids from libriform wood fibers in cases where the pits are only vaguely distinct.

Except for the presence of heterogeneous rays in wood of *Oldfieldia africana* specimen USW 19900 (Hayden, 1976), no other discrepancies were noted in Lebaq and Dechamps's (1964) description of this species. Likewise, specimens of *Oldfieldia, Celaenodendron, Piranhea, Irvingia, Klainedoxa*, and *Desbordesia* examined conform to descriptions in Record (1928, 1938), Webber (1936), and Metcalfe & Chalk (1950).

INFRAGENERIC VARIATION

Woods of the four specimens of *Picrodendron* examined show only small differences among themselves such as variation in the amount and distribution of axial xylem parenchyma. Furthermore, in comparison with the specimens from cultivation in Florida, wood of the Haitian specimen has a coarser texture (larger cells), greater average multiseriate ray height,

and more frequent vertically fused rays. These variations are not surprising, and probably reflect little more than the common observation that wood specimens from the same species will vary with position in the stem, age, and the growing conditions under which the wood was formed.

Likewise, leaves of the specimens examined are quite similar anatomically. There is, however, one aspect of leaf architecture that might be construed as evidence for more than one species of *Picrodendron*. Leaflets may have brochidodromous or reticulodromous venation (FIGURES 1, 2). Collections at the U. S. National Herbarium show that both of these venation patterns are frequent in the genus. However, brochidodromous and reticulodromous venation patterns seldom occur together in a single species (Leo J. Hickey, pers. comm.). The presence of a fimbrial vein in leaflets of *Picrodendron* is significant in this regard, since the occurrence of this structure is frequently correlated with pronounced variability in the dromy of the secondary veins (Hickey, pers. comm.). Thus, leaf architecture does not provide any convincing evidence for more than one species in the genus.

Leaflet outline varies somewhat in the specimens examined. According to Gillis (pers. comm.), leaflet form varies considerably throughout the populations which he examined. Patterns of leaflet variation which Small (1917) used to characterize the three species can no longer be relied upon owing to the foliar diversity in the specimens accumulated since his time.

No significant differences were discerned in nodal and petiolar patterns among the specimens available. Nodal and petiolar data presented here also agree very closely with the results of Richard A. Howard (pers. comm.).

There is, then, no sound anatomical evidence which could be used consistently to distinguish three separate species in the genus *Picrodendron*. On the contrary, the specimens examined are remarkably homogeneous, with the exception of their leaf morphology.

RELATIONSHIPS OF PICRODENDRON

Aside from the families discussed below, *Picrodendron* has also been associated with Terebinthaceae (Hallier, 1908) and Bombacaceae (Hallier, 1923). Terebinthaceae, as delimited by Hallier (1908), consisted of some Simaroubaceae, Anacardiaceae, and Engler's Juglandales, among other groups, most of which are discussed separately below. Bombacaceae and *Picrodendron* have little in common. Since Hallier (1923) presented no evidence to support such an association, a detailed discussion of possible relationships with Bombacaceae seems unnecessary here.

Relationships with Juglandaceae

From the evidence presented below, it seems apparent that much of the resemblance between *Picrodendron* and Juglandaceae is merely superficial. Shared in common are compound leaves, male inflorescences springing

from the previous year's growth (only some Juglandaceae), female flowers containing a bicarpellate ovary with a 2-lobed style, drupaceous fruits (only some Juglandaceae), and exendospermous seeds with a superior radicle. The morphological differences between *Picrodendron* and Juglandaceae are, however, numerous, the latter typically having the following characteristics: stipules absent; male flowers with tepals and rudimentary ovary; female flowers subtended by bracts; ovary inferior, one loculed above and 2–4 below; ovules one per locule, basal, orthotropous, with a single integument (Lawrence, 1951; Hutchinson, 1973; Willis, 1973). Furthermore, the pollen of *Picrodendron* is quite different from that of Juglandaceae (Erdtman, 1952; C. Rose Broome, pers. comm.).

Picrodendron and Juglandaceae are also quite dissimilar anatomically. One of the most typical features of leaves in the Juglandaceae is the presence of several different kinds of hairs, either simple, unicellular or uniseriate, or tufted: capitate glandular hairs are found in *Juglans,* and peltate glands with short unicellular or uniseriate stalks are a constant and characteristic feature for the family. Stomata are anomocytic. The vascular system of the petiole and midvein may be variously shaped and oriented, but possesses additional vascular strands on the adaxial side of the main cylinder (Metcalfe & Chalk, 1950). Leaves of *Picrodendron*, with their simple unicellular hairs, paracytic stomata, and petiole and midvein with simpler vasculature, differ greatly from leaves in Juglandaceae. These differences are further emphasized by the vertically transcurrent minor veins and vertically oriented spongy mesophyll cells in *Picrodendron.*

Kribs (1927), Heimsch and Wetmore (1939), Heimsch (1942), and Metcalfe and Chalk (1950) have studied wood anatomy in the Juglandaceae. In general, these authors report fiber-tracheids as the groundmass in all genera, scalariform perforation plates in some genera, a tendency towards ring porosity in other genera, and parenchyma that is chiefly in bands, diffuse and diffuse-in-aggregates parenchyma being found in only a few species. These woods differ strongly from the wood of *Picrodendron*, which is characterized by thick-walled imperforate elements approaching libriform wood fibers, exclusively simple perforation plates, pores more or less evenly distributed, and abundant diffuse and diffuse-in-aggregates axial xylem parenchyma.

On the basis of floral morphology, palynology, and anatomy, one must conclude that there is very little evidence for a relationship between *Picrodendron* and Juglandaceae.

Relationships with Simaroubaceae and other "Pinnatae"

It will be recalled that *Picrodendron* has been associated with the Sapindaceae, Anacardiaceae, Simaroubaceae, and Burseraceae. These families, along with Rutaceae and Meliaceae, comprise a conspicuous portion of a group of plants which Hutchinson called the "Pinnatae" (see Rock, 1972, for discussion of the placement of these families in various systems of

classification). This group of chiefly woody plants, as its name implies, is characterized by pinnately compound leaves. *Picrodendron*, with its trifoliolate leaves, resembles at least superficially many "Pinnatae." There are additional similarities in wood structure. Rock's (1972) survey of selected woods of this group points out the following characteristics: simple perforation plates, alternate intervascular pitting, imperforate tracheary elements with slit-like simple to slightly bordered pits, and "widespread presence of dark-staining, gum-like substances in the parenchyma and vessels . . ." In a discussion of five of these families (Sapindaceae was not included), Webber (1941) also noted vessel to ray pit-pairs that are in part half-bordered, and strands of crystalliferous parenchyma in many of these woods. Heimsch (1942) also noted many of the same characters in these families. The same features are also typical of *Picrodendron*, and this fact, together with its habit and frequent secretory cells (idioblasts) in the cortex, may indicate some sort of relationship between *Picrodendron* and the "Pinnatae."

Together, the six families of "Pinnatae" mentioned above account for about 6000 species of plants with various kinds of woody habits and floral structures. Because of the great number of plants involved, it is not difficult to find in diverse members of the "Pinnatae" floral features similar to many (but not all) of the features of *Picrodendron*. For example, plants with unisexual flowers or a reduced perianth or drupaceous fruits can be found in some parts of all "Pinnatae" families. Even an obturator can be found in Anacardiaceae and Meliaceae; the significance of this fact is not easily interpreted since, according to Davis (1966), in Anacardiaceae the obturator is of funicular origin and in Meliaceae, while of placental origin, it is composed of hairlike cells unlike the obturator of *Picrodendron*. It should be emphasized that these features are not constant, and that many "Pinnatae" are characterized by a biseriate perianth, bisexual flowers, various fruit types, and a lack of obturators. Further, some "Pinnatae" possess specialized features not found in *Picrodendron*: the lianous habit and peculiar stipules of some Sapindaceae; the zygomorphic floral symmetry in some Anacardiaceae, Rutaceae, and Sapindaceae; the staminal tube typical of Meliaceae; and the pellucid-punctate glandular leaves of the Rutaceae. Certainly the indefinite number of stamens in the male flowers and the absence of a floral disc in the flowers of both sexes of *Picrodendron* can be considered as evidence against a relationship to "Pinnatae."

Some outstanding anatomical differences between *Picrodendron* and "Pinnatae" include: secretory canals in the cortex, pith, or bark of various Anacardiaceae, Simaroubaceae, and Sapindaceae; secretory canals in the wood rays of many Anacardiaceae and Burseraceae; and the predominance of anomocytic stomata throughout most of the "Pinnatae" families under consideration. Secretory canals of either type are absent, and stomata are paracytic in *Picrodendron*. Before reaching any final conclusions about relationships with the "Pinnatae," one should consider the Simaroubaceae

in greater detail because so many botanists have placed *Picrodendron* in
or adjacent to this family.

When associated with the Simaroubaceae, *Picrodendron* is usually con-
sidered closest to three genera from tropical Africa and Southeast Asia;
namely, *Irvingia* Hooker f., *Klainedoxa* Pierre, and *Desbordesia* Pierre
ex van Tieghem. If these three genera are retained in Simaroubaceae, they
comprise the well-defined subfamily Irvingioideae Engler. Alternatively,
some authors (e.g., Hutchinson, 1973) place these genera in the family
Irvingiaceae [2] van Tieghem, while others (e.g., Willis, 1973) place them
in the Ixonanthaceae [2] Planchon ex Klotzsch, a small family having affini-
ties with the Linaceae.

One can only guess why Planchon (1846) associated *Picrodendron* with
the Simaroubaceae in the first place. Nevertheless, once it was placed in
this family, numerous anatomical similarities to the Irvingioideae were
discovered, thus strengthening the association despite the many morpho-
logical differences between *Picrodendron* and this subfamily. Anatomical
characters in common are paracytic stomata, palisade-like spongy meso-
phyll, vertically transcurrent minor veins, mucilage cells or spaces in the
cortex, and frequent crystals in the stem and leaf (Jadin, 1901; Solereder,
1908; Boas, 1913; Metcalfe & Chalk, 1950). On the other hand, *Picroden-
dron* lacks mucilage cells in the pith which are found in *Irvingia* and its al-
lies. Members of Irvingioideae differ from *Picrodendron* in having the fol-
lowing morphological characters: simple leaves, very large stipules, two
perianth whorls, bisexual flowers, a floral disc, a definite number of stamens
(10), 5–4 carpels (but 2 in *Desbordesia*), an undivided style, and only one
ovule per locule (Hutchinson, 1973).

The woods of *Picrodendron* and *Irvingia* and allies (as well as the
euphorbiaceous woods discussed herein) are also quite similar. These
woods are characterized by vessel elements with simple perforation plates,
alternate intervascular pitting, ray to vessel and/or parenchyma to vessel
pit-pairs ranging from half-bordered to simple, at least some parenchyma
in bands, very thick-walled imperforate tracheary elements with simple
or faintly bordered pits, multiseriate rays often vertically fused, parenchy-
ma cells frequently filled with an amber-colored substance, and sclerified,
crystalliferous, axial xylem parenchyma cells.

However, despite these overall similarities, the woods of *Irvingia*, *Klaine-
doxa*, and *Desbordesia* form a distinct and presumably natural group.
When they are compared with *Picrodendron*, the most noticeable difference
is the coarser texture of these woods: pores are mostly moderate-sized to
rather large (tangential diameter ranges from 114 to 285 μm.), vessel ele-

[2] According to ICBN (1972), Appendix II, Nomina Familiarum Conservanda, the
proper authorities for the family names Irvingiaceae and Ixonanthaceae are Exell and
Mendonça, presumably the first to use the names in the proper form for families.
The references as given on page 230 of the Code are: **Irvingiaceae** Exell et Men-
donça, Consp. Fl. Angol. 1: 279, 395. 1951 [Pierre, Bull. Mens. Soc. Linn. Paris 2:
1233. 1896 ('*Irvingiacées*')], and **Ixonanthaceae** Exell et Mendonça, Bol. Soc. Brot.
ser. 2a. 25: 105. 1951 [J. E. Planchon ex Klotzsch, Abh. Königl. Akad. Wiss. Berlin
1856: Phys. Abh. 235. 1857 ('*Ixionantheen*')]. *Ed.*

ments are mostly long (500–685 μm.), and imperforate tracheary elements (1368–2800 μm.) are medium-sized to very long (Webber, 1936). In addition, unilaterally compound pitting is often present between vessel elements and parenchyma cells, rays are somewhat broader, and ray cells are nearly all procumbent with a single row of square cells at the margin of the ray in the woods of Irvingioideae (Webber, 1936). Most of these differences, though, are merely details, and one must conclude that, as a group, *Picrodendron* and *Irvingia* and its allies are anatomically more homogeneous than are members of some well-defined and so-called natural families. (Compare, for example, the structural diversity present in Juglandaceae as mentioned above.)

As far as the relationships of *Picrodendron* are concerned, *Irvingia*, *Klainedoxa*, and *Desbordesia* pose a difficult problem since, on the one hand they are quite like *Picrodendron* anatomically and, on the other hand, they are markedly different morphologically. Because concepts of plant relationships are based primarily on floral morphology, it seems prudent in this case not to overweight the importance of anatomical evidence. Furthermore, *Irvingia* and its relatives are found exclusively in the Old World. In the absence of any other evidence for a relationship between members of the Irvingioideae and *Picrodendron*, it seems possible that the anatomical similarities of these plants are the result of convergent evolution. On the other hand, Webster (1967, and pers. comm.) thinks the Irvingioideae may be distantly related to Euphorbiaceae and, hence, also distantly related to *Picrodendron* (see below). Other subfamilies of the Simaroubaceae are even more different from *Picrodendron* than the Irvingioideae, both anatomically (Webber, 1936) and on the basis of floral morphology (Cronquist, 1944).

As far as a relationship to the "Pinnatae" in general is concerned, the position of *Picrodendron* is unclear. While its characters fall within the range of diversity of the "Pinnatae," *Picrodendron* would be a rather anomalous element of any family in the "Pinnatae" in which it might be placed. Differences do not seem too great, however, to preclude placing *Picrodendron* in its own family near or among the families of "Pinnatae," as was done by Scholz (1964) and by Takhtajan (1966).

Relationships with Euphorbiaceae

Fawcett and Rendle (1917) were first to propose a relationship between *Picrodendron* and Euphorbiaceae, saying, "The presence and form of the obturator at once suggested the family Euphorbiaceae and this affinity is borne out by other floral characters." Pax and Hoffmann (1931) excluded *Picrodendron* from Euphorbiaceae on the basis of its ovary (which they mistakenly thought to be inferior), lack of endosperm, and folded cotyledons. Palynological studies have largely been responsible for rekindling interest in a possible relationship between *Picrodendron* and Euphorbiaceae (Erdtman, 1952; Novák, 1961). Palynology has also proven useful in indicating affinities within the Euphorbiaceae; on this basis *Picroden-*

dron seems closest to the subfamily Oldfieldioideae Köhler & Webster (Webster, 1967 and 1975). Pollen of *Picrodendron* and certain genera of Oldfieldioideae are remarkably similar when viewed with either a scanning or a transmission electron microscope (Broome, pers. comm.).

Flowers of *Picrodendron* resemble those of the Euphorbiaceae more than those of its other putative relatives (see TABLE 2). Although the bicarpellate ovary, absence of a floral disc, and exendospermous seeds of *Picrodendron* are departures from "typical" Euphorbiaceae, these features are not unknown in the family. The pendulous, anatropous ovules with a placental obturator and the ventral raphe of *Picrodendron* present perhaps the strongest argument for its inclusion in the Euphorbiaceae, since this configuration is reputed to be the most constant and characteristic feature of Euphorbiaceae (Willis, 1973). *Picrodendron* is biovulate and has spinulose pollen, hence an affinity to the Oldfieldioideae seems likely. Although members of the Oldfieldioideae have diverse habits, *Celaenodendron* and *Piranhea* are trees with trifoliolate leaves which have a general resemblance to *Picrodendron*.

Relatively little is known about the anatomy of members of the Oldfieldioideae, unlike that of other putative relatives of *Picrodendron*. Metcalfe and Chalk (1950) examined only the primary structure of *Micrantheum* Desf., *Stachystemon* Planchon, and *Petalostigma* F. Mueller among the Oldfieldioideae. They mention very little specifically about these plants, all of which are Australian. The former two are ericoid in habit which is no doubt associated with anatomical specializations not necessarily characteristic of the trees and shrubs that make up most of the Oldfieldioideae. Nevertheless, paracytic stomata, vertically transcurrent small veins, and so-called "tanniniferous" cells occur commonly in the Euphorbiaceae (Metcalfe & Chalk, 1950) as well as in *Picrodendron*.

Metcalfe and Chalk (1950) examined seven genera of the Oldfieldioideae for wood structure. In general, these woods are characterized by simple perforation plates, alternate intervascular pitting, thick-walled fibers, heterogeneous rays mostly 2 or 3 cells wide, and banded and/or diffuse axial xylem parenchyma with some chambered crystalliferous cells, all of which are also typical of *Picrodendron*. Woods of *Picrodendron* and *Oldfieldia* are remarkably similar (Hayden, 1976). Aside from the similarities mentioned above and in the discussion of *Irvingia* and its allies, *Picrodendron* and *Oldfieldia* share the following characteristics: solitary pores about twice as frequent as radial multiples, pore clusters present only infrequently, intervascular pits which may have coalescent inner apertures, very similar heterocellular rays with some disjunctive cells, and multiseriate rays sometimes vertically fused. Furthermore, dimensions other than lengths of elements are similar in these woods. In contrast to the similarity between wood structures of *Picrodendron* and *Oldfieldia*, woods of *Celaenodendron* and *Piranhea* are more different. *Celaenodendron*, with its growth rings and small pores in predominantly long radial multiples, is distinctive. Both *Celaenodendron* and *Piranhea* have rays which are more homogeneous than those of *Picrodendron* or *Oldfieldia*, there being only a single row of

TABLE 2. Comparison of salient morphological features of
Picrodendron and Euphorbiaceae.

	Picrodendron	Euphorbiaceae
SEXUALITY OF FLOWERS	unisexual	unisexual
DISC	absent	present, usually
SEPALS	0 or 5	0 or 5
PETALS	0	0 or 5
STAMENS	3–many	1–many
OVARY	superior	superior
LOCULES	2	3, usually
OVULES	2/locule pendulous anatropous	1 or 2/locule pendulous anatropous
RAPHE	ventral	ventral
CARUNCLE OR OBTURATOR	present	present
FRUIT	drupe	schizocarpous capsule, more rarely a drupe
ENDOSPERM	none	present, usually

square or short erect cells at the margin. Bands of parenchyma are more pronounced in some specimens of *Piranhea* than in *Oldfieldia, Picrodendron*, or *Celaenodendron*. Differences between the woods of *Picrodendron* and *Oldfieldia* and those of *Celaenodendron* and *Piranhea* are nevertheless far outweighed by the similarities.

The pollen and wood structure of *Picrodendron* are so similar to those of *Oldfieldia* that one might expect these genera to be closely related. Unlike *Picrodendron*, however, *Oldfieldia* has opposite, digitately compound leaves and rather different inflorescences, flowers, and fruits. (Compare, for example, illustrations of these genera in Hutchinson, 1969).

CONCLUSION

In view of the basically euphorbiaceous structure of the flowers of *Picrodendron* and the numerous similarities of its wood anatomy and pollen to those of *Oldfieldia* and the Oldfieldioideae in general, this subfamily of Euphorbiaceae probably contains the closest living relatives of *Picrodendron*. Placing *Picrodendron* in the Euphorbiaceae-Oldfieldioideae would thus be preferable to aligning it with either Juglandaceae or any family of "Pinnatae." These conclusions are based upon evidence from three different and independent lines of investigation. Because of the dissimilar morphology of *Picrodendron* and *Oldfieldia*, and in agreement with Web-

ster (1975), these genera are probably best placed in separate tribes of Oldfieldioideae.

ACKNOWLEDGMENTS

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APPENDIX 1. Additional notes concerning Picrodendron specimens used in this investigation.

1) *Gillis 10893* — Collected by *David Fairchild* and *P. H. Dorsett 2846* on the Allison V. Armour Expedition; native of Jamaica, but collected from cultivation in Botanical Garden, Trinidad. P.I. 98559, M 5850.

2) *Gillis 10975* — Originally from seeds introduced by John Popenoe from Driggs Hill, South Andros, Bahamas; now plants with FTG #65–671; also *Gillis 11031* at FTG.

3) *Gillis 6963* — Cultivated on the estate of Mrs. Alvin Jennings, Coral Gables, Florida; source not known.

4) *Stadtmiller 171* (SJRW 19616) — This specimen, apparently unvouchered, was sent to Samuel J. Record at Yale through Mr. Stadtmiller from Service Technique du Département de l'Agriculture, Haiti, in 1931. A sample of this material was sent to Irma Webber in 1934 and is presumably that used in her "Systematic Anatomy of the Simarubaceae" (1936).

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FOSSIL DICOTYLEDONOUS WOODS FROM
YELLOWSTONE NATIONAL PARK

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Two regions of Yellowstone National Park contain successive horizons of silicified tree trunks, many in upright position, preserved in volcaniclastic rocks. The spectacular sequence of more than 25 forests at Specimen Ridge and Amethyst Mountain, along the south bank of the Lamar River in the northeastern region of the Park, was discovered by Holmes about a century ago. These fossil forests have been described by several authors including Knowlton (1899) and Dorf (1960, 1964). The lesser known but equally striking succession of fossil forests in the northwestern Gallatin area has been described by Andrews (1939) and Andrews and Lenz (1946). The fossil forests in the two areas, more than 40 miles apart, are in beds of approximately equivalent ages.

More than 100 species of fossil plants, 75 percent of them dicotyledonous, have been identified (Dorf, 1960, 1964) from beds along the Lamar River, chiefly from leaves in finer sediments of the formation containing the fossil forests. This leaf flora has predominantly warm-temperate and subtropical affinities but includes some forms with modern relatives in the tropics. Although the broad climatic implications of this Yellowstone flora are clear, MacGinitie (1974) has pointed out that Knowlton (1899) designated many of the fossil plants by names that are stratigraphic rather than botanical, and that, despite some updating by Dorf (1960), the Yellowstone flora is in need of revision. Consequently, the systematic affinities of many Yellowstone dicotyledonous plants remain in doubt.

Warmer climatic conditions than were probable for the Yellowstone fossil flora are suggested by the Kisinger Lakes flora (MacGinitie, 1974) from beds of similar age some 80 miles to the southeast in the Wind River Basin, Wyoming. This flora apparently lacks close botanical similarity to the Yellowstone fossil flora.

Despite the dominance of angiospermous taxa in the Yellowstone leaf flora, coniferous wood is more abundant than hardwoods in the fossil forests. Both types of wood have been described by Felix (1896), Knowlton (1899), Platen (1908, 1909), and Beyer (1954); Conard (1930), Read (1930), and Andrews (1939) described only conifers. Like the leaf flora, the Yellowstone dicotyledonous woods need re-examination. Only three of them have been studied in the last half-century (Beyer, 1954).

To investigate the identity of the angiospermous plants in the Yellowstone fossil forests, one of us (Scott) has made collections of dicotyledonous woods from Specimen Ridge and Amethyst Mountain along the Lamar River, and in the Gallatin area. To avoid harm to the remains of trees in place, only detached pieces were obtained from the slopes; conse-